OBSERVATIONS ON THE LONG-TERM POPULATION DYNAMICS OF THE PERENNIAL ASCIDIAN, *ASCIDIA MENTULA* O. F. MÜLLER, ON THE SWEDISH WEST COAST

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ABSTRACT

Six populations of *Ascidia mentula* O. F. Müller on subtidal vertical rock walls were monitored continually for 12 years (1971–1982) using stereophotographic techniques. Three stations at two depth levels were observed, along a hydrographical gradient extending 100 km from the sheltered inner parts of the Gullmarsfjord to the exposed archipelago off the Swedish west coast. Population densities increased during 1971–1976, and gradually declined from 1976. Recruitment was density-dependent while mortality was density-independent. Temporal covariation in recruitment between stations and depths separated fjord stations into two independent, correlated patterns: (1) the exposed archipelago station and the shallow semi-sheltered fjord station from (2) the shallow-sheltered fjord station from the sheltered and deep semi-sheltered fjord station. Temporal covariation in mortality separated the exposed station from the sheltered fjord stations suggesting different mortality factors. Histological analysis of gonads and analysis of photographically monitored recruitment revealed a seasonal reproductive pattern at 15 m depth while continuous reproduction and recruitment was observed in deeper populations. Temporal patterns of population density appeared to be related to long-term hydrographic changes mediated by variation in recruitment. Mortality caused by predation was not observed but disturbance and dislocation by sea urchins was an important mortality factor, especially at exposed sites.

INTRODUCTION

Study of fouling communities on submerged artificial substrates has contributed much to our knowledge of the structure and dynamics of subtidal epifaunal communities. However, the physical properties and the emplacement and subsequent handling of artificial substrates makes close comparison with natural substrates somewhat difficult (Dean, 1981; Kay and Keough, 1981; Schoener and Greene, 1981; Field, 1982). The development and regulation of communities established on artificial substrates have been of prime interest for investigators interested in such interactions as predation, competition and successional patterns (*e.g.,* Osman, 1977; Sutherland and Karlson, 1977; Karlson, 1978; Sutherland, 1981; Chalmer, 1982). These and other studies in the rocky intertidal (*e.g.,* Dayton, 1971; Menge, 1976) recognized the importance of seasonal and temporal variations in recruitment but, due to the relatively short term observations, inter-annual variation in recruitment have not been incorporated into explanations of the community structure.

The fauna of the rocky west coast of Sweden is greatly influenced by the Baltic current. This current is observed in the stratified water column as the upper, low salinity layer above a deeper, oceanic layer. Below the halocline the epifauna on the

granite rock walls is dominated by solitary ascidians, brachiopods, and tube-building polychaetes. Here annual ascidians temporarily reach high densities while perennial species show less pronounced fluctuations in density (Svane, 1983). *Ascidia mentula* O. F. Müller is a quantitatively important, perennial species found exclusively on hard substrates. It can reach high densities at depths greater than 15 m. It is rarely found above the 15 m level. *A. mentula* has a boreal-lusitanian distribution (Berrill, 1950) and is recorded as far north as the Trondheimsfjord on the west coast of Norway (Millar, 1966).

A detailed study of growth, reproduction, and long-term population dynamics of *A. mentula* at one station and depth is described by Svane and Lundälv (1981). The aim of the present study is to assess the role of reproduction, recruitment, and mortality in the spatial and temporal population dynamics of *A. mentula*. An attempt has been made to correlate changes in physical environmental parameters with patterns of recruitment, reproduction and mortality observed at three stations each at two depth levels over twelve consecutive years.

MATERIAL AND METHODS

A stereo-photogrammetrical analysis was undertaken on data obtained over a 12-year period (1971–1982) from three stations, each at two depth levels, on the Swedish west coast (Fig. 1). Station S1 is at an exposed locality (St. Sundskär 58°32.7′N, 11°3.3′E) in the Väderö archipelago off the Swedish west coast. Station G6 is in a
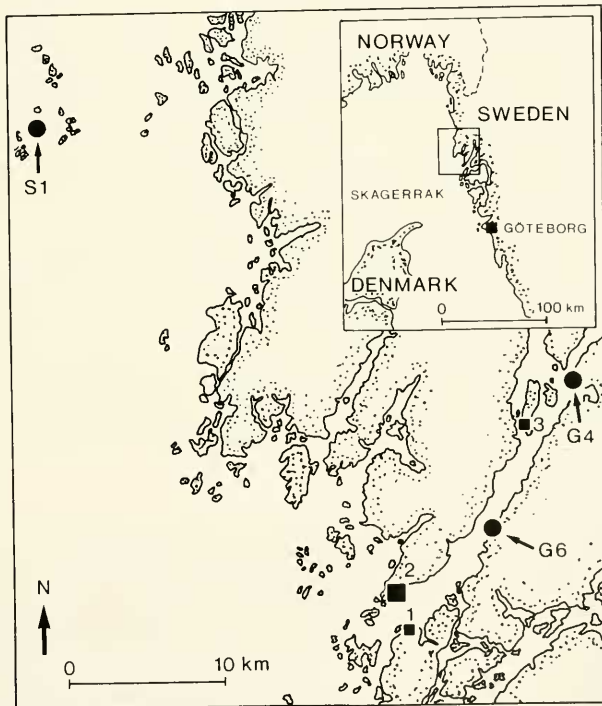

FIGURE 1. Map showing the Skagerrak area (inset) and the stations: S1: the exposed station in the Väderö archipelago. G6 and G4: the semisheltered and sheltered stations in the inner and central part of the Gullmarsfjord. 1. Kristineberg Marine Biological Station. 2. The town of Lysekil. 3. Bornö Hydrographical Station.

semi-sheltered locality (Gåsklåvan 58°23.7′N, 11°32.4′E) situated in the central part of the Gullmarsfjord. Station G4 is in a sheltered locality (Smörkullen 58°23.7′N, 11°37.9′E) situated in the inner part of Gullmarsfjorden. All stations are nearly vertical granite rock walls. Station S1 faces SSE and G6 and G4 face NW and W, respectively. The two depth levels at stations G4 and G6 were 15 m and 20 m; at station S1 they wee 20 m and 25 m. Observations of the 25 m site at station G6 and the 15 m site at station S1 do exist but *A. mentula* is not very common on the photographed areas. At station G4 the 20 m level is the deepest site as the fjord bottom is at 25 m depth. The rock walls at each site had the following mean inclination: S1, 20 m: 85°; S1, 25 m: 96°; G6, 15 m: 90°; G6, 20 m: 97°; G4, 15 m: 110°; G4, 20 m: 113°. At each station and depth level six test squares (a total area of 1.5 m^2) were inspected by SCUBA-diving and stereophotographed at regular intervals 3–7 times each year. The underwater photogrammetrical method and its limitations have been described by Lundälv (1971) and Torlegård and Lundälv (1974).

The population density, recruitment, and mortality figures were obtained by following individual animals throughout their observable benthic stages. Settling times and death, were estimated by interpolation between sampling dates and set arbitrarily at the middle of the period between two observations. Newly settled animals could be observed at a size of 2–3 mm, thus settling larvae and early postlarvae were not observed. Recruitment and mortality rates were calculated as follows: $r_{M,R} = \dfrac{X_{t_0-t_1}}{N_{t_0} \cdot \Delta t}$ where $X_{t_0-t_1}$ is the number which appeared or disappeared during the interval, N_{t_0} is the density at the start of the interval, and Δt is the time interval. Mortality rates and recruitment, calculated in one month intervals at the six locations, were tested for temporal covariation by correlation analysis (Sokal and Rohlf, 1981) and the correlation coefficients were clustered according to Mountford's (1962) method. Live material, for the study of reproduction and gonad histology, was obtained by regular diving during two periods and at two locations: during 1979 at Hågarnskär in the mouth of the fjord at 25 m depth as described by Svane and Lundälv (1981), and during 1980–1982 in the vicinity of station G6, in the central part of the fjord. Samples were obtained about every three weeks at station G6 at 15 m depth as in the 1979 study. The animals were fixed in Bouin's fluid and later transferred to 70% ethanol. The gonads were dissected out, embedded in Paraplast, cut into 8 μm sections, and stained in hematoxylin-eosin. The diameters of oocytes in one slide, all with the nucleolus showing in section, were measured for each ovary sample and the size frequency distribution in percent of total numbers was determined (see Giese and Pearse, 1974). Oocytes with a diameter above 125 μm were considered mature since no difference in staining or morphology was apparent in this size group.

Hydrographical properties of the study sites

Daily records of temperatures and salinities were obtained from Bornö Hydrographical Station (National Board of Fisheries, Sweden) for 15 and 20 m depths over the studied period. The recording station is located in the inner part of the Gullmarsfjord close to stations G4 and G6 (Fig. 1). Additional records (4–12 times per year, 1972–1977), were reported in Svane and Lundälv (1981) from Lysekil archipelago. Monthly mean temperatures and salinities are shown in Figure 2. Deviations from the monthly means were calculated at both depth levels and also depicted in Figure 2.

The study sites are influenced by two water masses, usually separated by a distinct halocline and often by a thermocline as well. The upper water mass is the so-called
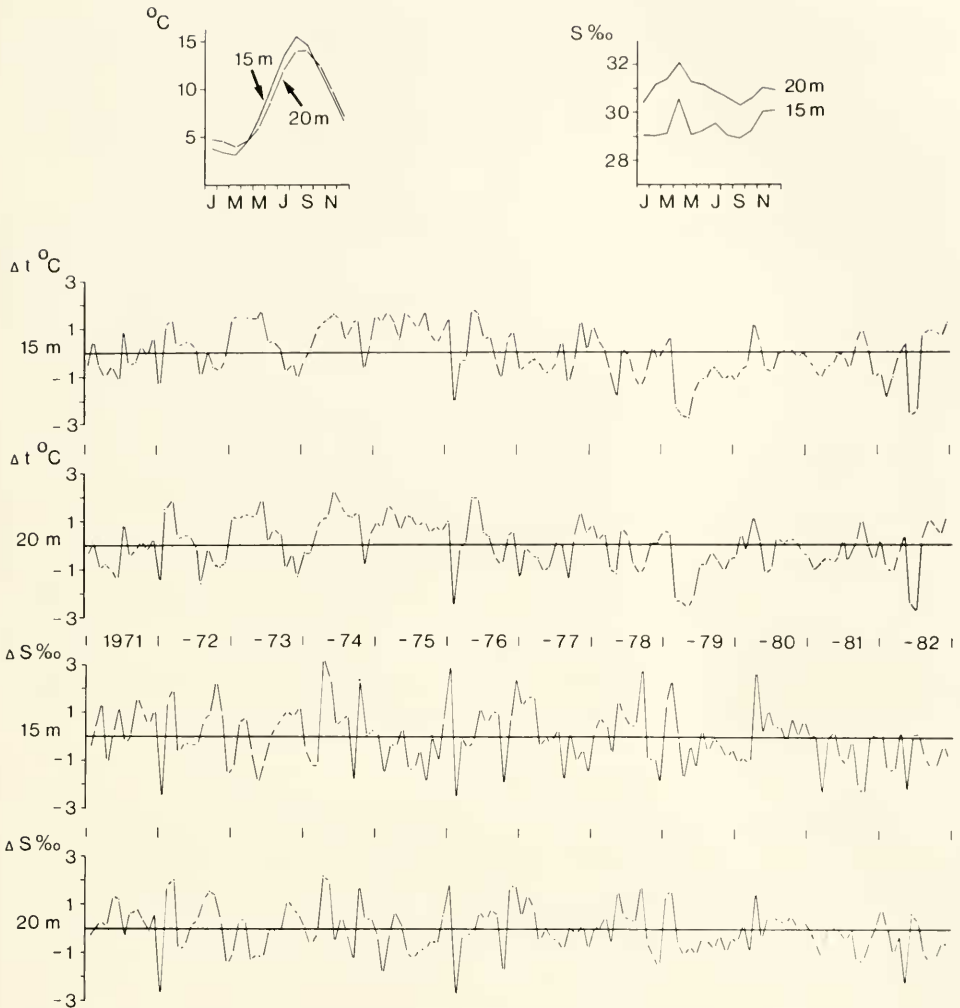
FIGURE 2.   Below: temperature and salinity anomalies at two depth levels (15 and 20 m) calculated as the mean monthly deviation from the 12-year mean. Above: mean yearly temperature (left) and salinity (right) patterns at two depth levels. Data from Bornö Hydrographical Station in the inner part of the Gullmarsfjord.

"Baltic-water," influenced by outflow from the Baltic Sea (S < 30‰). The lower water mass (S = 31–34‰) originates in the Skagerrak and is derived ultimately from the open North Sea. The discontinuity between these two water masses is normally found at depths between 10 and 15 m but is subject to rapid vertical displacements of considerable magnitude and may penetrate to a depth of 20 m (see Svansson, 1975).

Faunal components of the study sites

All the stations are dominated by ascidians. Other organisms, however, are constituents of the substratum on which the ascidian populations fluctuate.

On the exposed station S1 background organisms are mainly the tube building polychaete, *Pomatoceros triqueter* (L.), and the encrusting algae, *Lithothamnion* spp.,

which may cover the monitored areas extensively. Ascidians settle on and among these organisms. The annual ascidians are *Ascidiella scabra* (O. F. Müller), *Ascidiella aspersa* (O. F. Müller), *Corella paralellogramma* (O. F. Müller), and occasionally *Ciona intestinalis* (L.). The perennial ascidians include *Boltenia echinata* (L.) in addition to *A. mentula* as described by Svane and Lundälv (1981, 1982a) and Svane (1983). The sea urchins *Echinus esculentus* (L.) and *Echinus acutus* (Lamarck) are occasionally found and may leave tracks of ascidian-cleared substratum.

The sheltered stations in the fjord have a different composition and a more dense cover of epifaunal organisms. At the 20 m depth levels tube-building polychaetes dominate on the primary substratum. These are principally *Hydroides norvegica* (Gunnerus), *Serpula vermicularis* (L.), and *Chaetopterus variopedatus* (Reinier), and among these tubes the brachiopod *Crania anomala* (O. F. Müller). Patches of *Lithothamnion* spp. are also found, but considerably less than at the exposed sites. Together with *A. mentula* the relatively small perennial ascidians *Pyura tessellata* Forbes and *B. echinata* are fairly stable components at 20 m and deeper compared with the annual ascidians, as described by Svane and Lundälv (1982a, b). Within the fjord the annual ascidian *C. intestinalis* is abundant and shows large fluctuations in density. The small anthozoan *Protanthea simplex* Carlgren is common at both depths. At 15 m the cover of tube-building polychaetes is considerably less and brachiopods are only rarely found. At this depth patches of unidentified bluegreen algae occur and the small ascidian *Dendrodoa grossularia* (Van Beneden) is abundant. Sponges, mainly *Halicondria panicea* (Pallas) and *Haliclona* spp., are also found at both depths, but more commonly at the 15 m levels. Large sea urchins and carnivorous echinoderms are only rarely found, but the starfish *Asterias rubens* L. can be abundant, especially when *Ciona* populations are large (see Svane and Lundälv, 1982a; Svane, 1983).

RESULTS

Throughout the 12-year period of investigation the population densities varied in a similar fashion both among and within stations (Fig. 3). After initial low population densities in 1971, all increased to a maximum in the years 1975–1977, with the exception of station G4 at the 20 m depth which reached its lowest level in 1974, but thereafter followed the group pattern. After 1976–1977 all populations declined except for temporary increases in 1979 at station S1 and in 1980 at stations G6 and G4.

Spatial patterns

Recruitment. The number of recruits varied considerably both among and within stations. The yearly mean density and recruitment for each station and depth were calculated for the entire period of study (Fig. 4A) and showed a positive correlation (r = 0.93). A gradient of recruitment intensity at each depth level seems to exist with highest intensity at the exposed station S1 and successive reduction toward the inner part of the fjord. The positive correlation implies that larger populations receive proportionately more recruits. By expressing the recruitment rate as a function of population density (yearly mean values from the entire period of study), it is seen in Figure 4B that maximum recruitment rate was found at a population density of about 100 ind/m^2 above and below which the recruitment rate declines. Station G6, 15 m and S1, 25 m, showed reduced recruitment rates and may have reached their saturation levels. Station G6 and G4 at 20 m, however, were below their saturation levels.

Mortality. The mortality rate (yearly mean values from the entire period of study) was independent of density (Fig. 4C). Highest mortality rates were observed at the
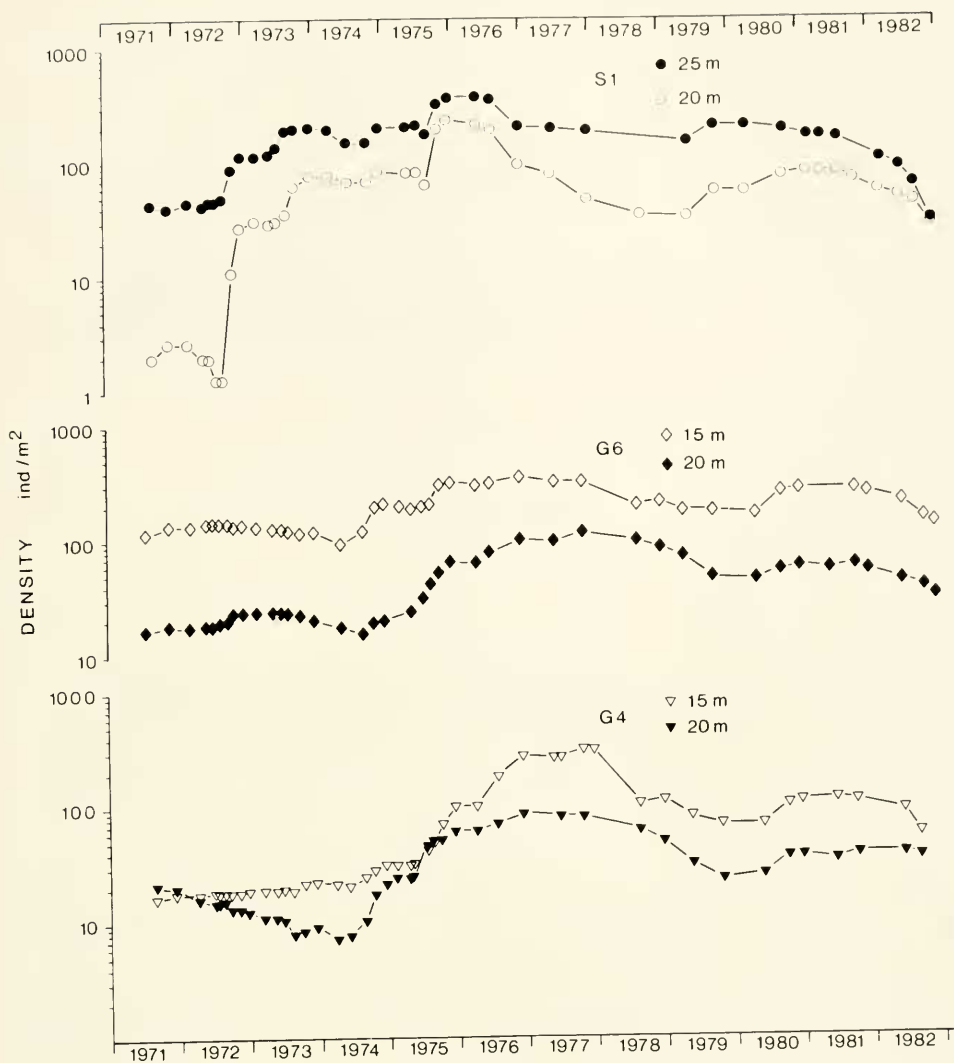
FIGURE 3. Densities of six populations of *Ascidia mentula* at three stations each at two depth levels (log scale). S1: the exposed station in the Väderö archipelago off the Swedish west coast. G6 and G4: the semi-sheltered and sheltered stations in the central and inner part of the Gullmarsfjord.

exposed station S1 (1 and 2) and lowest at the intermediate station G6 (3 and 4). The mean mortality rate was 40 ind/m²/year and recruitment consequently balanced mortality at two levels of density. A single individual at station G6, 15 m reached an age of 10.5 years, but maximum age at the remaining stations was about 8 years. However, the majority of individuals survived about two years.

No substantial predation was observed and dying animals were observed over long periods through lack of growth, shrinkage, and color-changing (see Svane and Lundälv, 1981). Mortality caused by disturbance and dislocation by sea urchins was important, especially at the exposed sites. Here browsing sea urchins were observed to "bulldoze" over the substratum and leave cleared tracks. When *A. mentula* was found in dense aggregates sea urchin activity was to some extent prevented since
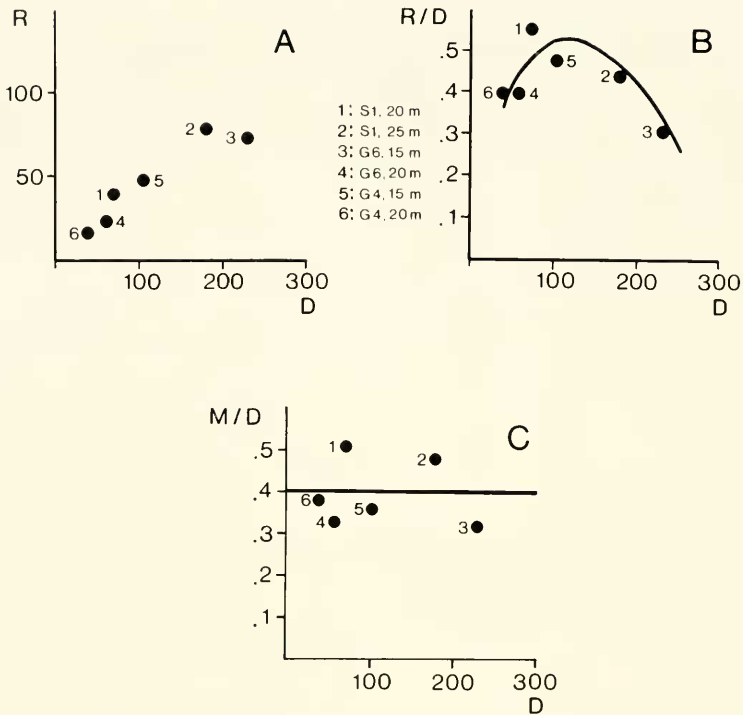
FIGURE 4. Recruitment (recruits/m²/year) (A) and recruitment rate (recruits/ind.) (B) and mortality rate (dead ind./ind.) (C) as a function of density (12-year mean values; each station and depth shown separately).

aggregates seemed to act as a rampart. Occasionally sea urchins carrying spine-stabbed ascidians were observed. At the sheltered sites large sea urchins were not common and relatively dense epifaunal cover restricted their movements and "bulldozing" effect.

Reproduction. Svane and Lundälv (1981) reported that *A. mentula* reproduced throughout the year with maximum intensity in October-November. Evidence was based on analysis of live material sampled at 25 m depth close to the mouth of the fjord (Fig. 5A). Later sampling performed at the 15 m level in the vicinity of station G6 in the central part of the fjord, revealed a seasonal pattern in oocyte size-frequency (Fig. 5B). At the 15 m depth level mature oocytes were only found from July to December with some seasonal differences between the two years studied, while at the 25 m level mature oocytes were found throughout the year. In animals sampled at 15 m, sperm were occasionally found in the gonoducts during the winter and spring (January–May), but no oocytes. At 25 m more than 50% of the animals carried oocytes or sperm (Svane and Lundälv, 1981). By summarizing monthly recruitment from the 12-year period of study the relative recruitment at each station and depth level was determined (Fig. 6). At the 15 m level (G6 and G4) very little recruitment took place during the winter months of January, February, and March compared to the other locations. Maximum intensity of recruitment occurred in September-October with the exception of station G4, 20 m, where maximum intensity occurred in July-August. At station G4, 20 m, recruitment was generally poor (Fig. 7).
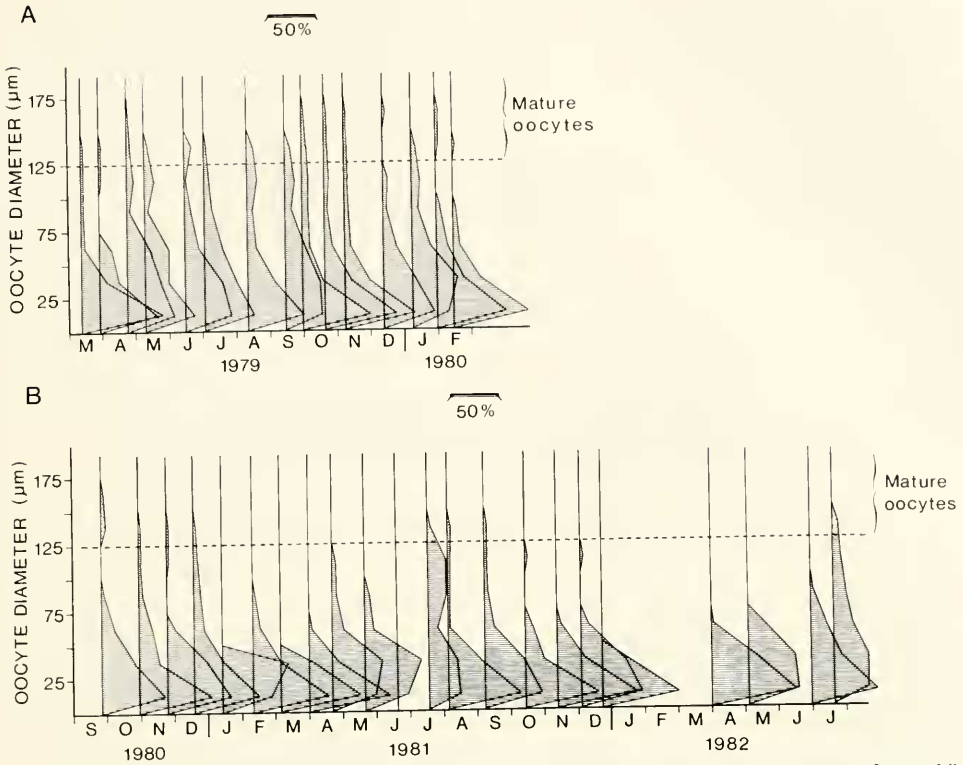
FIGURE 5. Oocyte size-frequency diagrams from two populations of *Ascidia mentula*. A: Hågarnsskär in the mouth of the Gullmarsfjord at 25 m depth. B: Gåsklåvan (the vicinity of station G6) in the central part of Gullmarsfjorden at 15 m depth. (Scale indicates 50% of total numbers in each sample).

Temporal patterns

The density patterns throughout the 12 years were similar although the stations are separated geographically by several kilometers (Fig. 1). However, recruitment and mortality factors were operating differently at different stations and depths. The overall
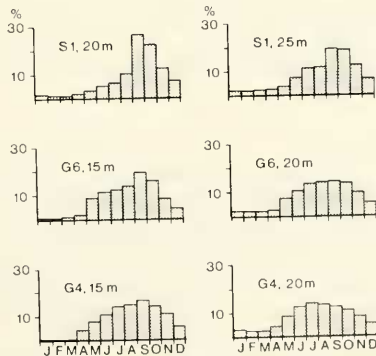

FIGURE 6. The mean recruitment at three stations each at two depth levels summarized from a 12-year period and calculated in one-month intervals.
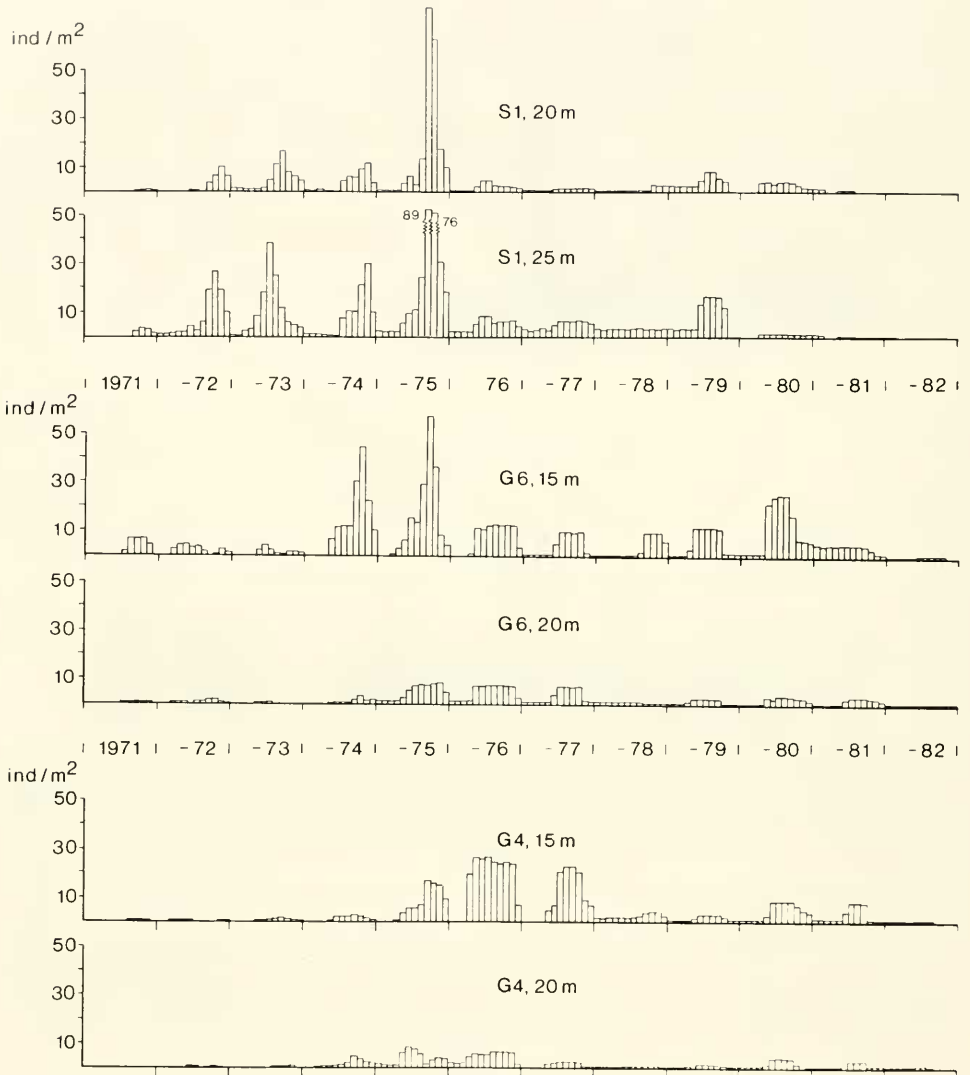
FIGURE 7.   Recruitment in six populations of *Ascidia mentula* at three stations each at two depth levels calculated in one-month intervals.

recruitment is depicted in Figure 7, showing the number of recruits observed at different stations and depths throughout the 12-year period of study, calculated in 1-month intervals. The overall mortality rates are depicted in Figure 8 as 6 month mean mortality rates. Both data sets were treated in a product-moment correlation analysis (Table I). Recruitment correlations separate significantly into two groups: station S1 and the shallow site at station G6 as one group and station G4 and the deep site at station G6 as another group (Table I). Thus the archipelago stations S1 and G6, 15 m in the central part of the fjord constitute one reproductively correlated pattern, while G6, 20 m, and station G4 in the inner part of the fjord, constitute another reproductively correlated pattern. However, significant correlation was also
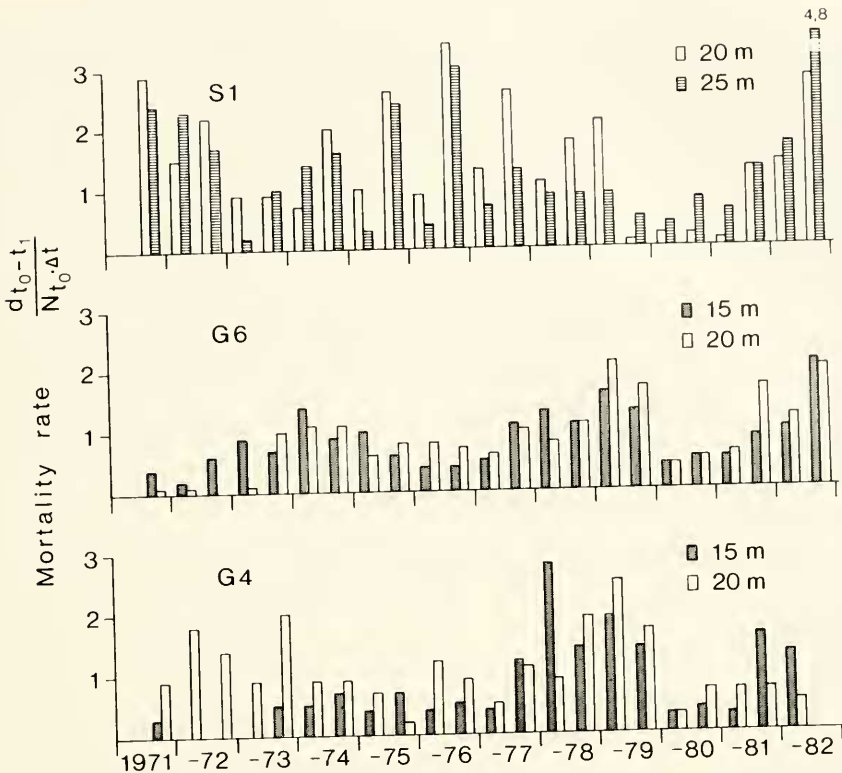
FIGURE 8. Mortality rates of six populations of *Ascidia mentula* at three stations each at two depth levels calculated as six-month means.

found between stations G6 and G4 at both depths, but at a lower level of correlation. In the fjord G6, 20 m, and the shallow site at G4 correlated highly while G4, 20 m, correlated with the other fjord sites less significantly.

Mortality correlations also separated significantly into two groups (Table I). Station S1 is separated and correlated negatively with the fjord stations G4 and G6, indicating that mortality factors were operating differently in the two areas. Stations G6, 20 m, and G4, 15 m, showed significant mortality correlations just as they did with respect to recruitment correlations. Both in recruitment as well as in mortality correlations G4, 20 m, showed some degree of separation from the other fjord stations but G4, 15 m, did not.

Temporal patterns and hydrography

The hydrographic observations (Fig. 2) showed noticeable variations during the 12-year study period. Winter temperatures at both depth levels during 1972–1976 were generally higher than the mean temperatures. In contrast winter temperatures were significantly lower during the years 1977–1982. Similar trends were not observed in the salinity data.

Temporal patterns of recruitment at station S1 and G6, 15 m showed some correlation to hydrography, while station G6, 20 m and G4 had comparatively low recruitment throughout the study period (Figs. 2, 6). Correlation between hydrography and mortality patterns were not apparent.
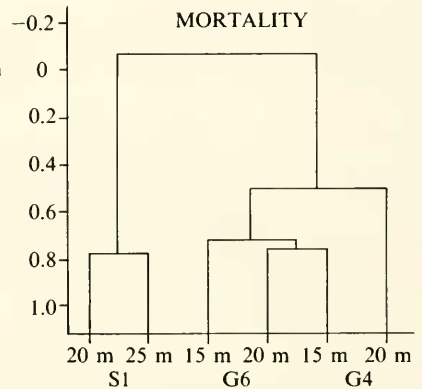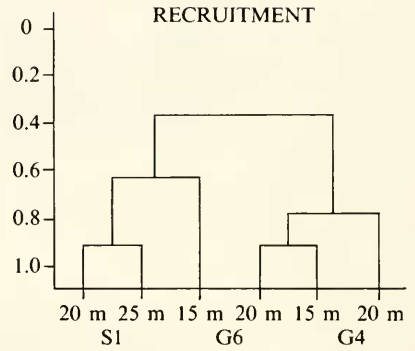
TABLE I

Correlation coefficients and cluster dendrograms of recruitment and mortality rates for A. mentula *at three stations each at two depth levels*

RECRUITMENT

		S1 20 m	S1 25 m	G6 15 m	G6 20 m	G4 15 m	G4 20 m
S1	20 m						
	25 m	0.911*					
G6	15 m	0.659*	0.617*				
	20 m	0.388*	0.412*	0.584*			
G4	15 m	0.253	0.251	0.433*	0.878*		
	20 m	0.152	0.177	0.502*	0.797*	0.714*	

* $P < 0.01$

MORTALITY

		S1 20 m	S1 25 m	G6 15 m	G6 20 m	G4 15 m	G4 20 m
S1	20 m						
	25 m	0.772*					
G6	15 m	−0.079	−0.302				
	20 m	−0.050	−0.147	0.690*			
G4	15 m	0.049	−0.103	0.693*	0.699*		
	20 m	0.083	−0.061	0.347	0.348	0.213	

* $P < 0.01$

DISCUSSION

Recruitment patterns

The positive correlation between recruitment and density may have several explanations:

Attraction of larvae to adults. Attraction of marine invertebrate larvae to adults of the same species occurs in barnacles (Knight-Jones and Crisp. 1953), polychaetes (Wisely, 1960), molluscs (Knight-Jones, 1951), echinoderms (Young and Chia, 1982), and ascidians (Young and Braithwaite, 1980). Larvae of *A. mentula* may occasionally settle on the cuticle of adults but the great majority settle on the substratum among adults. Preliminary experiments failed to demonstrate any attractive effect of adult ascidians on larvae when separated by a plankton-net. If adults attract larvae chemotactically the stimulus must be weak. Figure 4B shows that the recruitment rate increased with population density up to about 100 ind/m², above which the rate decreased. The possibility that at high adult densities larvae may be trapped, and consequently destroyed, in the branchial sac of the adults cannot be ruled out.

Local settlement and dispersal. Thorson (1964) suggested that the larval life of ascidians is so short that they will remain mainly in the surroundings where they

were born and so settle among their parents. The correlation analysis (Table I) suggests that recruitment took place locally.

The length of the planktonic larval life of *A. mentula,*and many other solitary ascidians evidently lasts no more than a few hours and probably only a few minutes. Thorson (1946), did not find significant ascidian larvae among the ½ million planktonic larvae identified in his comprehensive study of the larvae of bottom invertebrates of the Øresund. In the group called "other larvae of bottom invertebrates" which constituted 4.5% (see Thorson, 1946, p. 373), ascidian larvae did not seem to be of importance. Ascidians are, however, common in the Øresund (Dybern, 1967; Lützen, 1967).

Along the Swedish west coast and in the fjords where ascidians are quantitatively abundant Erikson (1973) and Ölundh (1977) rarely found ascidian larvae. The same condition obtained in the Gullmarsfjord plankton (Lönning, 1962; Lindahl and Hernroth, 1983; Hernroth, pers. comm.) although adult populations of several thousand per m² can be found (Svane, 1983). Dybern (1965) did find larvae of *Ciona intestinalis* (L.) in plankton samples from a shallow (3–5 m), narrow sound. He concluded that these larvae were from local populations of considerable size. Lützen (1960), in an attempt to collect larvae of the winter breeding *Styela rustica* (L.) in the Gullmarsfjord during its peak reproductive season, found only 27 larvae among several liters of plankton examined.

The length of the pelagic life of ascidian larvae varies, ranging from a few hours to several days (Millar, 1971). In cultures at 15°C in constant dim light where the only substrate was plankton-net or PVC-aquarium walls, the planktonic larval life of *A. mentula* ranged from a few minutes to 240 hours. Fifty percent of the larvae had metamorphosed after 120 hours. When offered a suitable granite rock larval life was considerable reduced. The larvae seemed potentially able to metamorphose shortly after hatching. The swimming ability of *A. mentula* larvae was, however, very poor and no uniform directional movements towards a light source could be recognized (pers. obs. To be reported in detail elsewhere). In nature, therefore, the distribution of larvae must be governed by water movements. Swimming ability may play a role only very close to the substratum. Other species (*Ciona intestinalis, Corella paralellogramma, and Pyura tessellata*) have a shorter larval life under similar laboratory conditions.

The dispersal of recruits occurs first by passive transport of eggs and, after hatching, by passive transport and active swimming of larvae. When an egg is released into sea water the follicle cells expand osmotically and increase their buoyancy (Berrill, 1975). The eggs, however, must be kept in suspension by water movements to avoid sinking. The development time of the eggs is temperature-dependent (Goodbody, 1974, Berrill, 1975) *e.g.,* 30 hours at 15°C (pers. obs.). Therefore, distribution of the larvae of solitary oviparous ascidians, must occur mainly during the period from egg spawning to hatching.

Protection of postlarvae and juveniles. Large populations may protect postlarvae and juveniles. Buss (1981) showed that the bryozoan *Bugula turrita* settled gregariously and preferentially in selected locations where resident density was high or intermediate and that the interspecific competitive ability of *B. turrita* was density-dependent. Dense aggregates of *A. mentula* to some extent prevent sea urchin activity by providing a barrier and thereby reducing mortality within aggregates. Continuous recruitment into established aggregates may prolong longevity in that single individuals may be more easily removed from the substratum. The recruitment rate, however, was density-dependent (Fig. 4B) but the mortality rate density-independent (Fig. 4C). Consequently, this result does not support the idea of Buss (1981) that formation of aggregates in

sessile organisms is caused by density-dependence in settlement reflected by density-dependence in mortality.

At station S1 unoccupied substratum always seemed available, apparently due to sea urchin activity. At station G6 open or unoccupied substratum was sparse but at the 15 m level high densities and high recruitment was observed (Figs. 4, 7). Likewise at station G4 unoccupied substratum was apparently sparse but the epifaunal cover of other organisms was somewhat less than at G6. Some sea urchin activity at the fjord stations was observed but it was considerably less than that at station S1. Figure 4B may indicate that at station G6, 15 m, and S1, 25 m, where recruitment rates were relatively low compared to the high population densities, substratum was a limiting factor during most of the period of study.

Light and substratum orientation. Light infuenced settlement of marine invertebrate larvae (Thorson, 1964) and some ascidians may respond in their settling behavior to light (Grave, 1935; Crisp and Ghobashy, 1971), but many do not (Grave, 1941; Thorson, 1964; Young and Braithwaite, 1980). Ascidians are generally found in shaded situations *e.g.,* the underside of rocks and boulders and below overhangs on rock walls (Dybern, 1963; Crisp and Ghobashy, 1971). At station S1, *A. mentula* is most commonly found below overhangs, somewhat less frequently on vertical rock-surfaces, and not at all on horizontally orientated substrates. Preferential settlement on shaded substrates may explain this pattern, but sea urchin activity may have a similar effect. At the fjord stations G6 and G4, where sea urchin activity was less, *A. mentula* was more evenly distributed. Yet even here *A. mentula* is not found on horizontal substrates. Sedimentation on horizontal substrates may restrict recruitment and subsequent survivorship.

Finally, orientation of the substratum to light and water currents may be important in settlement as in barnacles (Crisp and Barnes, 1954; Crisp and Stubbings, 1957). Station G6, where the highest population density was found at the 15 m level, is situated in the central and most narrow part of the Gullmarsfjord (Fig. 1). The vertical rock walls are densely covered with filter-feeding organisms and large fluctuating populations of the annual *Ciona intestinalis.*

Synchrony in recruitment

Synchrony in settling of intertidal barnacles and molluscs can occur over distances of hundreds of kilometers (*e.g.,* Lewis *et al.,* 1982), although considerable local variations both in space and time can occur (Lewis and Bowman, 1975; Southward, 1967). Keough (1983) found no synchrony in recruitment of sessile invertebrates onto pannels at two subtidal sites in southern Australia and regarded recruitment as a stochastic process. Recruitment of *A. mentula* showed variations among stations and depths (Fig. 7) but correlation analysis revealed a distinct pattern grouping the archipelago sites with the mid-fjord shallow site and the inner fjord sites with the mid-fjord deep site (Table I). The hydrographical properties of the fjord may play an important role in the separation. Mixing of coastal, "North Sea water" with fjord water at the depths in question may occur less frequently in the inner parts of the fjord, especially when the common westerly winds blow surface water into the fjord, where it become relatively isolated.

Reproduction

The reproductive pattern of *A. mentula* reported by Svane and Lundälv (1981) is consistent with the results from this study, at depths greater than 15 m where reproduction occurs throughout the year (Figs. 5, 6). However, at the 15 m levels,

reproduction was seasonal (Fig. 5) with no significant recruitment during winter months. This suggests that larvae may settle at the same depth level as the spawning populations from which they originally arose (Fig. 6).

Temperature is important in gonad maturation and larval development in ascidians (Goodbody, 1974; Berrill, 1975). Mean winter temperatures were considerably lower at 15 m than at 20 m and summer temperatures were somewhat higher at 15 m compared to 20 m (Fig. 2). Comparatively lower winter temperatures and high summer temperatures seemed to induce the seasonal reproductive pattern. Maximum recruitment intensity within the year was similar at all stations and depths, with the exception of G4, 20 m, where maximum intensity took place in July-August. However, it was comparatively low throughout the period of study (Fig. 6).

Mortality

No relationship was found between the mean population density and mortality rate (Fig. 4C) and consequently mortality was density-independent. Possibly density-independent factors operated during the transition from warm to cold periods, with density-dependent factors operating during other periods (Figs. 2, 8). The temperature change in 1977 may have influenced the mortality at the exposed station S1 but no effect was observed at the sheltered stations G6 and G4. Equally, the increased mortality observed at the sheltered stations during 1978–1979, where temperatures were below the mean (Fig. 2), was not observed at station S1 although mortality was relatively high at the 20 m level. When separating the individual stations and depths no correlation was found between yearly mean mortality rate and population density.

The gradient of exposure from station S1 towards the fjord stations was reflected in the mortality rates although within the fjord the rates were higher at the inner station G4 than at station G6 in the mid-fjord.

No substantial predation on *A. mentula* was observed, either in the photographs or during the numerous dives (Svane, 1983). A detailed study of survivorship based on single generations was not meaningful at most stations due to continuous recruitment. At station S1, 25 m, however, the generation time was relatively short and separation of generations was possible. Svane and Lundälv (1981) studied this population during an 8-year period and found that increased mortality correlated with increased reproductive activity but dislocation and disturbance by sea urchins may sometimes be an important mortality factor.

Mortality factors operated differently at different stations. At station S1, where sea urchin activity and a harsh physical environment play important roles, mortality was high. At station G4 and especially at station G6 mortality was comparatively low. The local environment may play an important role. Station G6 is located in the most narrow part of the fjord (Fig. 1) and prevailing currents may provide better food supply. In the fjord in general large sea urchins are sparse and their activity is limited due to dense epifaunal cover.

Temporal patterns and hydrography

Power spectra, from Fourier analysis, of mean annual sea temperatures from the Plymouth area demonstrated a dominating 5-year cycle (Maddock and Swann, 1977). This cycle may be related to the 5-year cycle in monthly mean temperatures from Bornö Hydrographical Station shown in Figure 2. The temperature pattern and the shift in monthly mean temperatures during 1976–1977 was consistent with temperature recordings from the deepest part (700 m) of the Norwegian Trench (Norwegian Fisheries

Board, Flödvigen) and was therefore representative for most of the North Sea and Northeast Atlantic.

The impact of the "warm period" during 1972–1976 on benthic communities in the North Sea area has been shown by Buchanan *et al.* (1978) and Beukema *et al.* (1978) but is not apparent in the long-term investigations of the German Bight presented by Zigelmeier (1978). Gray and Christie (1983) reviewed some long-term studies of benthic populations showing an increase in density during the "warm period" but attributed these changes to 6–7 year cycles. They concluded that many species do respond to long-term hydrographic cycles.

Species with southerly distribution patterns should benefit from elevated winter temperatures and increase in numbers and northerly distribution (Southward *et al.,* 1975). *A. mentula* has a boreal-lusitanian distribution and should thus be favored. The population densities in Figure 3 may be attributed to this pattern. All populations increased in numbers during the "warm period," with some minor fluctuations, and then gradually decreased during the following "cold period."

Recruitment was intensive during the "warm period" (1972–1975) at stations S1 and G6, 15 m, with very high numbers in 1975 (Fig. 7). At stations G6, 20 m, and G4 no important recruitment, however, was recorded during the first four years of the "warm period" but recruitment increased during 1975, 1976, and 1977. During the preceeding "cold period" important recruitment was observed at all stations in a somewhat scattered pattern and was most intensive at stations G6, 15 m, and S1, 25 m. Evidently, recruitment could not be entirely related to temperature variations. Some trends, however, should be noted. The high recruitment in 1975 coincided with unusually high mean temperatures throughout the year. Lower temperatures observed in January 1976 and spring 1979 and the first "cold period" winter temperatures in 1977 (Fig. 2) may be traced in the recruitment patterns (Fig. 7) because very little recruitment took place during these periods.

However, mortality showed no apparent correlation to hydrography and the fjord stations varied in a somewhat contradictory pattern when compared with the archipelago station S1 (Fig. 8). During the cold winter and spring 1978–1979, however, elevated mortality rates were observed at stations S1, 20 m, G6, and G4 but during 1980–1981 mortality was low at all stations and depths with no apparent correlation to temperature or salinity (Figs. 2, 8).

Large-scale temperature cycles and local variations may influence the population density of *A. mentula* by increased recruitment at elevated temperatures but sheltered populations may respond differently. Mortality of adults was regulated locally and temperature independent within the range discussed.

ACKNOWLEDGMENTS

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